Developmental Dimorphism: Consequences for Larval Behavior and Dispersal Potential in a Marine Gastropod

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Abstract. Specific effects of alternative developmental programs on swimming and settlement behavior for marine larvae have not been identified experimentally. A major impediment to this research has been the rarity of species with variable development. Here, we compared traits related to movement and habitat selection for different ontogenetic stages of long-lived, feeding larvae (planktotrophic) and short-lived, nonfeeding larvae (lecithotrophic) of the herbivorous gastropod *Alderia modesta*. Newly hatched planktotrophic larvae swam in meandering paths with equal rates of upward and downward movement. As planktotrophic larvae developed towards competence (physiological ability to metamorphose), their swimming paths became straighter, faster, and increasingly directed towards the bottom, traits shared by newly hatched lecithotrophic larvae. Despite differing in developmental history, competent planktotrophic (32-d-old) and lecithotrophic larvae (competent upon hatching) exhibited qualitatively similar swimming behaviors and substrate specificity. However, lecithotrophic larvae moved downward at twice the speed of competent planktotrophic larvae, potentially producing a 5-fold higher rate of contact with the bottom in natural flows. Competent larvae swam downwards rather than passively sinking, even though sinking rates were faster than swimming speeds; active swimming may allow larvae to keep the velum extended, permitting rapid response to chemical settlement cues and promoting successful habitat colonization. Differences between larvae of the two development modes may reflect fine-tuning by selection of traits important for dispersal and settlement into patchy adult habitats.

Introduction

Many organisms express threshold traits that result in discrete forms differing in morphology, life history, or behavior (Roff, 1996). Such dimorphisms often confer a dispersal advantage on one morph over the other. Numerous examples are known for insects (Harrison, 1980; Zera and Denno, 1997), including winged *versus* wingless aphids (Dixon, 1985), crickets (Crnokrak and Roff, 1995, 1998), plant-hoppers (Denno *et al.*, 1980, 1996), and water striders (Fairbairn and Desranleau, 1987). Some plants produce both nondispersing seeds and seeds that are adapted for increased dispersal from the parent (Payne and Maun, 1981; Morse and Schmitt, 1985; Venable, 1985; Venable and Levin, 1985). In salamanders, paedomorphosis results in an aquatic adult, while metamorphosis produces legged adults that can migrate over land (Semlitsch *et al.*, 1990). One morph generally has a selective advantage over the other under a given set of environmental conditions, but carries a fitness cost (Roff, 1996). The migratory form can locate new food patches or mates, but often has a lower reproductive potential as a trade-off (Denno *et al.*, 1980; Roff, 1986, 1996; Semlitsch *et al.*, 1990; Langellotto and Denno, 2001).

Although well studied in terrestrial organisms, dispersal dimorphisms have received less attention among marine invertebrates (Raimondi and Keough, 1990; Hadfield and Strathmann, 1996). For many benthic marine species, significant dispersal is achieved only during the free-swimming larval stage (Strathmann, 1985, 1990; Levin and Bridges, 1995; Pechenik, 1999). In a few species, some offspring metamorphose prior to hatching, while their siblings hatch and swim into the water column (Gibson and Chia, 1995; Chester, 1996). Intra-clutch differences in set-

tlement requirements may also function as dispersal dimorphisms, with some larvae settling quickly and nonselectively while the rest disperse until encountering a specific environmental cue (Krug, 2001; Toonen and Pawlik, 2001). An extreme dispersal polymorphism occurs in species that produce both feeding (planktotrophic) and nonfeeding (lecithotrophic) larvae in the same population (Levin, 1984; Krug, 1998). The rarity of such species has generally precluded intraspecific comparisons between long- and short-lived larval morphs, however (Hoagland and Robertson, 1988).

The evolutionary significance and biological consequences of planktotrophy *versus* lecithotrophy have long been debated (Thorson, 1950). Planktotrophic larvae are generally much longer-lived than lecithotrophic larvae, often resulting in populations that are demographically open and genetically homogeneous over large areas (Scheltema, 1962; Caley *et al.*, 1996; Todd, 1998). In contrast, lecithotrophic species often show strong genetic differentiation over short spatial scales (Palumbi, 1995; Hellberg, 1996; Todd, 1998; Todd *et al.*, 1998). Demographic effects of development mode may reflect trade-offs between adult fecundity and offspring survivorship (Levin and Bridges, 1995). For habitat selection, models predict that a longer competency period exposes larvae to a larger number of potential settlement sites (Doyle, 1975, 1976); planktotrophic species may offset the costs of dispersal through extended competency and rapid response to cues of habitat suitability (Obrebski, 1979; Pechenik, 1999). An alternative strategy is to limit dispersal from patchy habitats by producing short-lived larvae, thus ensuring local colonization (Todd, 1998; Pechenik, 1999). Lecithotrophic larvae appear unable to extend their competency period without suffering severe post-metamorphic consequences (Pechenik, 1990, 1999), and may exhibit behaviors that minimize dispersal during a brief pelagic interval (Todd, 1998; Todd *et al.*, 1998).

Alternative developmental pathways must ultimately produce a competent larva, but how developmental differences affect the evolution of larval swimming and settlement behavior remains largely unexplored. As Wieczorek and Todd (1998) remarked, "considering only larvae at the attainment of competence, it is probably an article of faith amongst larval biologists that the settlement and metamorphic behaviors of pelagic lecithotrophic species are not fundamentally different from those of species that reproduce by means of planktotrophic larvae." Experimental investigations are clearly needed to test such assumptions. The sea slug *Alderia modesta* (Lovén, 1844) is the only mollusc known to produce both planktotrophic and lecithotrophic larvae in one population (Krug, 1998). After hatching, planktotrophic larvae of *A. modesta* mature for 4 weeks to reach competence, the stage at which larvae are able to settle and metamorphose (Krug and Zimmer, 2000). In contrast, lecithotrophic larvae are competent immediately upon hatching (Krug, 2001). This species thus provides an opportunity to examine the consequences of different development modes on the behavior of distinct but conspecific larval types. A specialist herbivore, *A. modesta* is found in temperate estuaries exclusively upon yellow-green algae of the genus *Vaucheria* De Candolle (Xanthophyta: Xanthophyceae) (Hartog and Swennen, 1952; Bleakney and Bailey, 1967; Trowbridge, 1993). Larvae of *A. modesta* metamorphose in response to bioactive carbohydrates from the adult host alga, *V. longicaulis* Hopp (Krug and Manzi, 1999). A dissolved form of the settlement cue triggered immediate changes in swimming behavior of both larval types; chemically stimulated larvae altered their swimming speeds and increased turning rates, exhibiting site-restricted searches during settlement (Krug and Zimmer, 2000).

In the present study, swimming behavior, physical characteristics, and settlement specificity were compared for the two developmentally distinct larval types of *Alderia modesta*. Our aim was to determine whether development period, which profoundly changes dispersal potential, also results in differences between the two larval types that might affect their distribution in the water column or settlement opportunities. Physical and behavioral characteristics that affect larval movement, such as speed and direction of swimming, were measured for planktotrophic larvae of different ontogenetic stages and for lecithotrophic larvae of several ages. This study is a first step towards linking swimming behaviors associated with alternate dispersal strategies to key components of habitat colonization such as transport, delivery to the bed, and settlement.

Materials and Methods

Collection of organisms and larval culture

Specimens of *Alderia modesta* and patches of *Vaucheria longicaulis* were collected from Mission Bay, a shallow estuary located in San Diego, California, 21 km north of the border between the United States and Mexico. The remaining natural wetlands are confined to the Kendall-Frost Marine Reserve and Northern Wildlife Preserve in the northeastern corner of the back bay. Adult *A. modesta* were collected from mats of *V. longicaulis* on the reserve mudflat. Seawater from the Scripps Institution of Oceanography aquarium was filtered to 0.45 μm (FSW) prior to use.

Several hundred specimens of *A. modesta* were placed in petri dishes overnight, sufficient time for each slug to produce one clutch. Egg masses identified as planktotrophic or lecithotrophic (Krug, 1998) were separated and maintained in FSW, which was changed every other day until hatching. Lecithotrophic larvae from about 50 egg masses were pooled and transferred to fresh FSW upon hatching; larvae were subsampled for use in experiments the next day. From 80–100 planktotrophic egg masses were hatched together

for each batch culture, and the resulting pool of larvae was divided into replicate beakers containing 3 l of FSW at concentrations of 1 larva per milliliter. Aliquots from uni-algal suspensions of the phytoplankton *Rhodomonas* sp., *Isochrysis galbana,* and *Pavlova lutheri* were added in a 1:1:1 ratio to cultures to give a final concentration of about 10^4 cells per milliliter. Every 2–3 days, larvae were sieved through a 52-μm mesh and transferred to clean FSW with fresh phytoplankton. Cultures were stirred by pipetting water against the bottom twice daily but were otherwise static. Competence was tested by periodically exposing 10 plank-totrophic larvae from a batch to the inductive alga *V. longicaulis* and scoring metamorphosis after 2 d. Larvae did not attain competence earlier than day 26, and the majority became competent after 30 d in culture (Krug and Zimmer, 2000). Experiments were performed promptly after larvae reached competence; replicate trials were conducted using batches cultured in December 1999 and in July 2000.

Quantitative measurements of swimming behavior

Larval swimming behavior was quantified in light and dark for 8-, 16-, and 32-d-old planktotrophic larvae, and for 1-, 2-, and 4-d-old lecithotrophic larvae (larval age is days since hatching from the egg mass). Swimming paths were imaged with a Cohu infrared-sensitive video camera having a Pentax 100-mm macro lens. All video recording was done at 22 °C, using only infrared light for dark treatments. In light trials, an incandescent bulb (GE Daylight Ultra) was placed within a baffled housing to provide diffuse light. An Ocean Optics, Inc. (model S2000) spectroradiometer was connected to a miniature fiber optic probe, and light was measured underwater in an experimental chamber at the same position as video observations of larvae (see below). The mean photon flux (140 μE/m^{2}s), spectral composition (intensity peaks between 435 and 543 nm), and angular distribution (sharp decline in intensity between 40° and 50° relative to the zenith) in the chamber were similar to morning sunlight in a shallow estuary (Lythgoe, 1979; Forward *et al.,* 1984).

Behavioral assays were performed in chambers (3 × 3 × 5 cm) at a concentration of 5 larvae per milliliter. Under these conditions, sufficient swimming paths were recorded over 30 s to permit statistical comparisons between treatments. A total of 8–10 replicates were run for all age classes, using different larvae in each replicate. To minimize the likelihood of recording the same larva more than once, the field size was limited to 0.6 (height) × 0.8 (width) × 0.3 (depth) cm, less than 0.5% of the total chamber volume. All images were captured with the middle of the field placed at 1.5 cm above the bottom, and with the focal plane in the center of the chamber. These images were processed at 10 frames per second through a computer-assisted video motion analyzer (CAVMA) (Motion Analy-

sis Corp. model VP 320, ExpertVision, and custom software) interfaced with a Sun Microsystems SPARC 2 computer workstation.

Analysis consisted of determining the vertical component (*Y*-dimension only) and total swimming speed for each path of larvae initially suspended in the water column (see methods in Tamburri *et al.,* 1996). Because measurements of speed are scalars, they contain no information on the direction of larval movement. For each path, we therefore subtracted the distance moved downwards from the distance moved upwards, and divided the difference by time to quantify the rate of net vertical displacement as a vector. This quantity may be the most relevant measure relating patterns of swimming and sinking to dispersal and settlement, as it indicates whether an individual tends to move up, down, or remain in suspension. Larval movement was also expressed as net-to-gross displacement (NGD), the ratio of the linear distance from the starting to the ending point in a given path to the total distance traveled. The NGD ratio thus measures the tendency of paths to be circular or twisted; values range from zero, for a path with origin and endpoint at the same spatial coordinates, to a maximum of 1.0 for paths that are completely straight. Ratios were arcsine-transformed to normalize the data before statistical analysis.

To ensure that swimming behavior was not affected by chamber size or larval density, four replicate trials were performed in a 10 × 10 × 20 cm chamber at a concentration of 0.3 larva per milliliter. Lecithotrophic larvae were equil-ibrated in the chamber for 3 h in the light, prior to video recording for 1 h. They were subsequently held in darkness for 3 h, before an additional 1 h of filming under infrared (IR) illumination. Video records were made with the middle of the field of view (1.5 × 1.8 cm) located 15 cm above the bottom, and with the focal plane in the center of the chamber. Swimming behavior was quantified by CAVMA and compared with data from the 3 × 3 × 5 cm chamber by unpaired two-tailed student's *t*-tests. No difference in total swim speed was found for larvae in large (1.16 ± 0.05 mm/s, $n = 80$) and small (1.24 ± 0.04 mm/s, $n = 202$) chambers ($P > 0.20$). Similarly, vertical speeds ($P > 0.35$) and net vertical displacement rates ($P > 0.75$) also did not differ between chambers. Moreover, the concentration of larvae in the small chamber did not affect behavioral assays, as collisions were never observed. Results were thus inde-pendent of larval density and chamber size over the ranges tested. Small chambers were used in subsequent experi-ments because of limitations in available larvae.

Responses to light and dark

Behavior following a change in illumination was mea-sured for 8-, 16-, and 32-d-old planktotrophic larvae and 1-d-old lecithotrophic larvae, to test whether shadow re-

sponses were present (Young and Chia, 1985) and whether they differed according to age or development mode. For each age class, 40 larvae per replicate were placed in the recording chamber and observed within a 0.6 × 0.8 cm field of view, running 5–10 replicates per class. Larvae were acclimated in the light for 10 min, and were then recorded for 1 min in the light treatment. The light was next extinguished, and larvae were recorded for 1 min in darkness under IR illumination only. The full-spectrum light was then turned back on, and behavior was recorded for an additional 1 min. Through subsequent viewing of the video recordings, the number of larvae observed was scored every 15 s for the full 3 min of each trial. To test for interactions between age class and light/dark treatment, a two-way ANOVA was performed. The number of swimming larvae in each of the four age classes was compared for the following three time points: (1) after 15 s in the initial light treatment, (2) 15 s after the transition to darkness, and (3) 15 s after reexposure to light.

Size and gravitational fall velocity

Planktonic larvae are often modeled as passive particles, vertically distributed by sinking or turbulent mixing. To evaluate the contribution of passive (gravitational fall) *versus* active (swimming) movements to downward transport, sinking rates were measured for precompetent (8-d-old) and competent (32-d-old) planktotrophic larvae, for 1-d-old and 4-d-old lecithotrophic larvae, and for the empty shells of 1-d-old lecithotrophic larvae. Individuals were narcotized in seawater containing excess $MgCl_2$ for 5 min; larvae were then washed twice with seawater and introduced into a temperature-controlled fall velocity apparatus consisting of two nested acrylic plastic chambers (Hannan, 1984). An inner chamber (15 cm square by 40 cm tall) was elevated 5 cm above the bottom and 5 cm below the top of an outer chamber (30 cm square by 50 cm tall); both were filled with 1-μm filtered seawater and equilibrated to 22 °C. Larvae added through a snorkel at the top of the inner chamber were video recorded during the middle 20 cm of their descent. Time from addition through the snorkel to passage through the field of view was about 3 min; controls showed that larvae remained narcotized for more than 5 min after rinsing in fresh seawater, and motion analysis of the video confirmed that larvae were sinking straight downward and not swimming during these measurements. Paths were analyzed using CAVMA to obtain terminal sinking velocities.

The sizes of larvae were also compared. Empty shells were collected after competent planktotrophic ($n = 48$) and lecithotrophic ($n = 89$) larvae had completed metamorphosis, and arranged on a depression slide such that shells lay on their side. The maximum shell dimension was measured on a compound scope using a calibrated ocular micrometer,

accurate to ± 3 μm. Precompetent larvae were anesthetized ($n = 36$) prior to shell measurements after 8 days in culture.

Substrate selection and metamorphosis

Larvae of benthic organisms must leave the water column and contact the bottom to colonize new habitats, either initiating metamorphosis or rejecting the encountered substratum and reentering the plankton. A 48-h bioassay was used to compare the metamorphic response of 32-d-old planktotrophic larvae and 2-d-old lecithotrophic larvae to the natural host, *Vaucheria longicaulis*, and four other species of macroalgae. *Enteromorpha clathrata* and *Ulva expansa* co-occur with *V. longicaulis* and thus represent potential habitat cues, whereas *Chaetomorpha linum* and *Codium fragile* are hosts for other local ascoglossan species (Abbott and Hollenberg, 1976). For each treatment, 10–15 larvae were added to each of three replicate dishes containing 4 ml of FSW and a branchlet of a given alga, cleaned of epiphytes. Negative controls were FSW.

Results

Swimming behavior of larvae differing in age and developmental history

Total swimming speed, NGD, and vertical speed were quantified for precompetent planktotrophic larvae after 8 and 16 d in culture, for 32-d-old competent planktotrophic larvae, and for lecithotrophic larvae 1, 2, and 4 d after hatching (Table 1). Within each age class, no significant difference was detected between light and dark treatments for a given behavioral characteristic (Scheffé test: total speed, $P > 0.99$; NGD, $P > 0.46$; vertical speed, $P > 0.99$). There was also no difference in swimming speed, NGD, or vertical speed between batches from different seasons ($P > 0.05$ for each characteristic), indicating that results were not batch-dependent or seasonal (Table 2). Data for light and dark, and from different batches, were therefore pooled prior to statistical comparisons between classes. Lecithotrophic larvae exhibited the highest values for total speed, NGD, and vertical speed, while precompetent larvae had the smallest values for each trait. Competent, 32-d-old planktotrophic larvae consistently exhibited intermediate values. Lecithotrophic larvae of all ages swam significantly faster than 8- and 16-d-old planktotrophic larvae (one-way ANOVA: $F_{5,833} = 12.4$, $P < 0.0001$; Scheffé test, $P < 0.005$). Competent larvae generally swam at similar total speeds, regardless of age or developmental history; the only significant difference was between 2-d-old lecithotrophic and 32-d-old planktotrophic larvae (Scheffé test, $P < 0.05$).

In addition to speed, the trajectories of larval swimming paths may substantially affect distributions in the water column. Precompetent larvae generally swam in meandering paths, whereas competent larvae made primarily vertical

Table 1

Mean (± SE) swimming speeds and net-to-gross displacement (NGD) for planktotrophic and lecithotrophic larvae

Larval class	Total speed (mm/s)		NGD ratio		Vertical speed (mm/s)	
	Light	Dark	Light	Dark	Light	Dark
Planktotrophic						
8-day	0.94 ± 0.07	0.85 ± 0.05	0.74 ± 0.04	0.83 ± 0.03	0.44 ± 0.06	0.42 ± 0.06
16-day	0.79 ± 0.12	0.92 ± 0.09	0.88 ± 0.03	0.85 ± 0.03	0.58 ± 0.15	0.57 ± 0.09
32-day	1.14 ± 0.09	1.03 ± 0.09	0.85 ± 0.02	0.84 ± 0.02	0.73 ± 0.11	0.65 ± 0.07
Lecithotrophic						
1-day	1.22 ± 0.05	1.21 ± 0.04	0.90 ± 0.01	0.92 ± 0.01	1.06 ± 0.12	0.92 ± 0.06
2-day	1.34 ± 0.09	1.42 ± 0.10	0.88 ± 0.02	0.88 ± 0.02	0.97 ± 0.10	1.05 ± 0.15
4-day	1.14 ± 0.07	1.32 ± 0.07	0.88 ± 0.03	0.90 ± 0.03	0.74 ± 0.12	0.99 ± 0.12

NGD is a ratio of the linear distance from the first to the last point of a given path to the actual distance traveled; a value of zero indicates a circle, whereas a ratio of 1.0 represents a straight line. Vertical speed is a measure of larval movement in the Y-dimension only.

excursions, swimming mainly upwards or downwards (Fig. 1). To quantitatively describe this behavior, NGD ratios were calculated for larval paths. Lecithotrophic larvae of all age classes had significantly higher NGD ratios than 8-d-old planktotrophic larvae (Table 1, and results of a one-way ANOVA: $F_{5,707} = 9.2$, $P < 0.0001$; Scheffé test, $P < 0.05$). The three ages of planktotrophic larvae did not significantly differ from each other in NGD (Table 1).

Total swimming speeds do not necessarily indicate the capacity of larvae to control their position; the vertical component of swimming speed better represents the ability of a larva to move selectively downward during settlement. Lecithotrophic larvae of *Alderia modesta* swam only about 1.4 times faster than 8-d-old planktotrophic larvae in terms of total speed, but were 2.3 times faster in the vertical

dimension (Table 1). Vertical speeds varied significantly among larval classes (one-way ANOVA: $F_{5,651} = 14.1$, $P < 0.0001$). Lecithotrophic larvae had significantly faster vertical speeds than 8-day-old and 16-d-old planktotrophic larvae (Scheffé test, $P < 0.05$), but did not differ from competent planktotrophic larvae (Scheffé test, $P > 0.10$). Competent planktotrophic larvae had significantly faster vertical swimming speeds than 8-d-old precompetent larvae (Scheffé test, $P < 0.05$). Lecithotrophic larvae thus swam in the straightest, fastest paths, and competent larvae of both types moved significantly faster in the vertical dimension than precompetent larvae.

Larvae changed their position in the water column as they developed and became competent to settle. Newly hatched planktotrophic larvae distributed themselves evenly

Table 2

Mean (± SE) swimming speeds and net-to-gross displacement (NGD) ratios for independently reared batches of competent planktotrophic and lecithotrophic larvae

Larval batch	Total speed (mm/s)		NGD ratio		Vertical speed (mm/s)	
	Light	Dark	Light	Dark	Light	Dark
Planktotrophic (32-d)						
Dec. 1999	1.20 ± 0.12	1.16 ± 0.16	0.86 ± 0.04	0.85 ± 0.04	0.95 ± 0.23	0.70 ± 0.20
July 2000	1.04 ± 0.14	0.93 ± 0.09	0.83 ± 0.03	0.84 ± 0.03	0.60 ± 0.10	0.64 ± 0.07
P value	0.40	0.20	0.13	0.59	0.50	0.45
Lecithotrophic (1-d)						
Nov. 1999	1.25 ± 0.07	1.24 ± 0.04	0.90 ± 0.02	0.94 ± 0.01	1.14 ± 0.20	0.93 ± 0.07
June 2002	1.18 ± 0.08	1.14 ± 0.07	0.89 ± 0.02	0.90 ± 0.02	0.97 ± 0.11	0.88 ± 0.09
P value	0.20	0.50	0.37	0.10	0.99	0.93

Planktotrophic larvae were cultured for 32 d and tested during the indicated month. NGD ratios represent the relative straightness of larval paths and were arcsine transformed for comparisons. Vertical speed measures larval movement in the Y-dimension only; data were normalized by the function $\ln(x + 0.01)$ prior to statistical analyses.
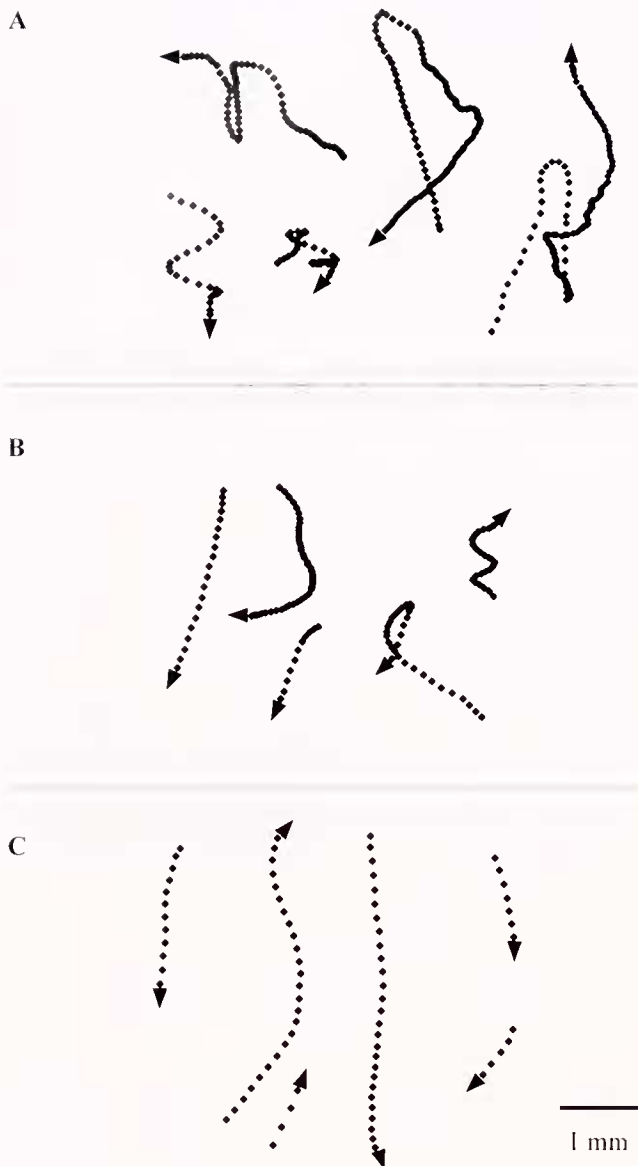
A

B

C

1 mm

Figure 1. Representative paths of larvae swimming off the bottom in filtered seawater. Data are computer-digitized video records of vertical paths as viewed from the side of a chamber. Each path of dots represents the position of a given larva at consecutive two-frame intervals with video collected at 10 frames per second. The same scale bar applies to all paths. (A) Representative paths of precompetent, 8-d-old planktotrophic larvae, showing the frequent turns and meandering movement typical of immature larvae. (B) Paths of competent, 32-d-old planktotrophic larvae. Larvae increasingly swam towards the bottom in straighter, faster paths as they matured to competence. (C) Swimming behavior of competent, 1-d-old lecithotrophic larvae. Paths show the rapid, vertically oriented swimming that characterizes nonfeeding larvae of *Alderia modesta*.

throughout the water column and did not respond to changing light regimes (Fig. 2A). As planktotrophic larvae neared competence, the trend was for fewer larvae to swim off of the bottom (Fig. 2B). Most competent, 32-d-old planktotrophic larvae remained on the bottom in initial light treat-

ments, as did 1-d-old lecithotrophic larvae (Fig. 2C, D). Competent larvae of both development modes displayed a striking shadow response: both 32-d-old planktotrophic larvae and 1-d-old lecithotrophic larvae immediately swam up into the water column following a transition to darkness (Fig. 2C, D). After 1 min, most larvae settled out of the water column and returned to the bottom, where they remained during a subsequent exposure to light. The effects of age and photostimulation on larval position in the water column were tested using a two-way ANOVA (Table 3). Light or dark treatment had a significant effect on the number of swimming larvae ($P < 0.0001$), and the interactive term for light treatment *versus* larval developmental class was also significant ($P < 0.005$). This result reflects the fact that both competent types responded to alternating light and dark regimes, whereas precompetent larvae were indifferent to changing light conditions.

Role of larval swimming *versus* sinking in vertical transport

Mathematical models of settlement rates are generally based in part on larval (or "particle") characteristics, including gravitational fall velocities or swimming capabilities. Sizes and sinking rates were thus determined for competent planktotrophic and lecithotrophic larvae, and for precompetent, 8-d-old planktotrophic larvae, as a measure of how the three classes compared as passive particles. No difference was found between 1-d-old lecithotrophic larvae and 32-d-old planktotrophic larvae in mean maximum shell dimension, a measure of size (Table 4). Similarly, when competent larvae were anesthetized and introduced into a specially constructed chamber, the two types gave the same mean sinking rate (Table 4). Compared to precompetent larvae, both types of competent larvae were significantly larger (Table 4, and results of a one-way ANOVA: $F_{2,170} = 1081.7$, $P < 0.0001$; Scheffé test, $P < 0.0001$) and sank significantly faster (Table 4, and results of a one-way ANOVA: $F_{2,41} = 11.5$, $P < 0.0001$; Scheffé test, $P < 0.005$).

In terms of time budgets, a similar proportion of precompetent larvae swam downward (57%) as upward (G test for goodness-of-fit: $G = 0.41$, df $= 1$, $P > 0.50$). The mean rate of net vertical displacement for precompetent larvae, -0.13 mm/s, was not significantly different from a null-expectation of zero net movement (one-tailed t-test: $t = 1.1$, df $= 19$, $P > 0.20$). On average, immature feeding larvae thus exhibited behaviors expected for dispersing propagules that must remain suspended in the water column to feed during development. In contrast, significantly more competent planktotrophic (71%; $G = 8.11$, df $= 1$, $P < 0.01$) and lecithotrophic larvae (85%; $G = 27.96$, df $= 1$, $P < 0.001$) swam down towards the bottom, compared to the 50%:50%
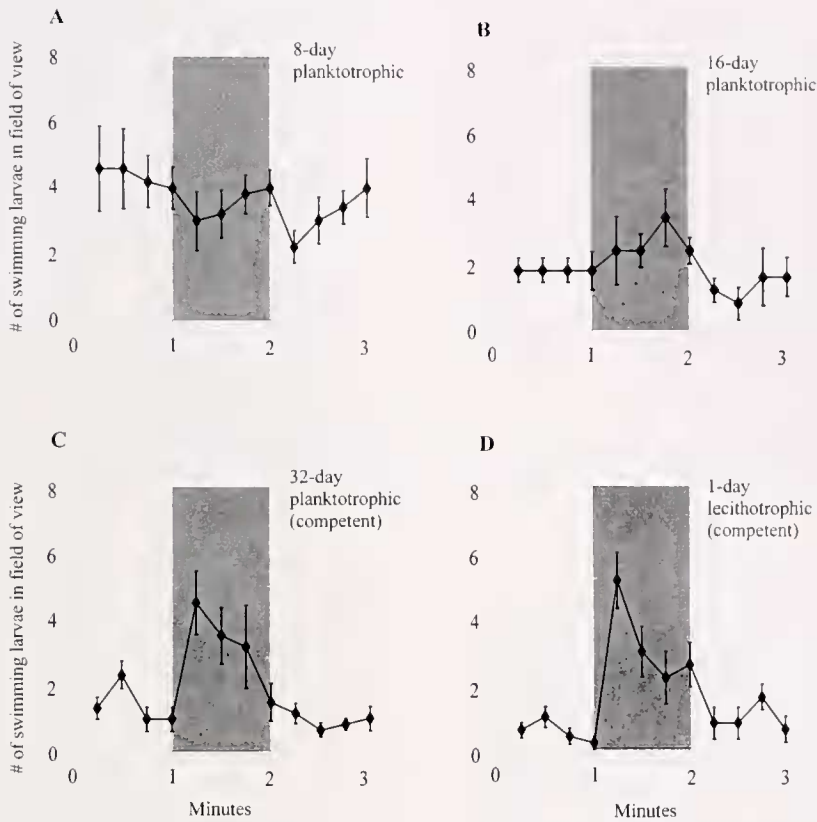
Figure 2. Mean number ($\pm$ 1 SE) of larvae observed swimming off the bottom in response to light and dark, within a 0.6 $\times$ 0.8 cm field of view. Shading indicates observations made in the dark. (A) 8-d-old (precompetent) planktotrophic larvae, in alternating light and dark regimes. (B) 16-d-old (precompetent) planktotrophic larvae. (C) Competent (32-d-old) planktotrophic larvae. (D) 1-d-old lecithotrophic larvae. which are competent upon hatching.

ratio expected for a null-model of equal upward and downward movement. This significant bias in direction, combined with greater speeds and straighter paths, resulted in significant rates of downward displacement for lecithotrophic larvae (one-tailed t-test: $t = 8.3$, df = 57, $P < 0.0005$) and competent planktotrophic larvae (one-tailed t-test: $t = 4.0$, df = 46, $P < 0.0005$) (Table 4).

Table 3

Results of a two-way ANOVA comparing effects of (1) light versus dark exposure, and (2) developmental age and type (class), on larval position in the water column

Source of variation	df	SS	MS	F_s	P
Light treatment	2	53.03	26.52	10.61	0.0001
Developmental class	3	18.67	6.22	2.49	0.071
Treatment $\times$ class	6	55.63	9.27	3.71	0.004
Error	48	120	2.50		
Total	59	247.33			

Data are the number of larvae observed swimming off the bottom within the video field (0.6 $\times$ 0.8 cm) of an experimental chamber.

Competent planktotrophic larvae and 1-d-old lecithotrophic larvae were comparable in size and sinking rate (Scheffé test, $P > 0.90$), and showed similar patterns of downward movement. After 4 d, lecithotrophic larvae sank at a significantly slower rate (Scheffé test, $P < 0.005$), closer to that of empty lecithotrophic shells (-0.88 ± 0.04 mm/s). Older nonfeeding larvae expended their yolk reserves and lost tissue mass during their planktonic period, which likely lowered their density and hence sinking rate. Lecithotrophic larvae of both ages had a significantly faster rate of net vertical displacement than precompetent planktotrophic larvae (one-way ANOVA: $F_{3,195} = 6.5$, $P < 0.005$; Scheffé test, $P < 0.05$). Competent planktotrophic larvae were intermediate in their rate of net vertical displacement, due to swimming behaviors that tended to keep live larvae suspended off the bottom despite a high sinking rate. For all larval classes, video observations revealed that larvae moving straight downward were actively swimming with the velum extended, as opposed to passively sinking with the velum withdrawn as in the gravitational fall chamber.

Table 4

Comparison of mean (± SE) shell sizes, gravitational fall velocities, and net vertical displacement for larvae differing in age and developmental type

Properties	Precompetent	Competent		
	8-day-old planktotrophic	32-day-old planktotrophic	1-day-old lecithotrophic	4-day-old lecithotrophic
Passive properties:				
Shell size (μm)	126 ± 1[a]	194 ± 1[b]	194 ± 1[b]	193 ± 2[b]
Gravitational fall velocity (mm/s)	−0.90 ± 0.09[a]	−1.59 ± 0.12[b]	−1.52 ± 0.10[b]	−0.99 ± 0.10[a]
Active properties:				
Net vertical displacement (mm/s)	−0.10 ± 0.08[a]	−0.40 ± 0.12[ab]	−0.78 ± 0.09[b]	−0.73 ± 0.21[b]

Unlike speeds, which are nondirectional scalar values, net vertical movement is a vector with negative values indicating movement towards the bottom. Statistical comparisons for each larval characteristic were performed using a one-way ANOVA with *post hoc* Scheffé tests. Within each row, means labeled with the same letter did not differ significantly (*post hoc* comparison, α = 0.05).

Substrate selection and metamorphosis

To compare substrate selectivity between larval types, competent (32-d-old) planktotrophic and 2-d-old lecithotrophic larvae were exposed to five algal species (Fig. 3). For both larval types, the adult host *Vaucheria longicaulis* induced significantly higher levels of metamorphosis than all other algae (one-way ANOVA: $F_{11,24} = 22.0$, $P < 0.0001$; *post hoc* Scheffé tests, $P < 0.005$). There was no difference

% metamorphosis

Figure 3. Mean (+1 SD) percent metamorphosis of competent, 32-d-old planktotrophic larvae and 2-d-old lecithotrophic larvae in response to the host alga, *Vaucheria longicaulis*, and four other algae. Means joined by a vertical bar did not differ significantly (one-way ANOVA followed by *post hoc* Scheffé tests, $P > 0.98$).

in the response of planktotrophic and lecithotrophic larvae to *V. longicaulis*, and no other alga triggered more metamorphosis than FSW controls. Only low levels of spontaneous metamorphosis (1 ± 1%) occurred in cultures of planktotrophic larvae prior to assays.

Discussion

Consequences of swimming behavior and ontogenetic stage for larval transport

The transport and distribution of larvae fundamentally influences patterns of dispersal and settlement, processes that regulate population dynamics and community structure of marine benthic invertebrates (Roughgarden *et al.*, 1988; Pechenik, 1999). To understand how hydrodynamics affect settlement rates, larvae have been modeled as sediment particles, with sinking or swimming speeds used to describe larval movements (Gross *et al.*, 1992; Eckman *et al.*, 1994). Larvae are maintained in suspension by turbulent eddies; high turbulence mixes larvae away from the bed and low mixing allows sinking. Models predict maximal settlement when larvae become concentrated near the bottom due to low turbulent mixing or high downward flux of larvae. Some studies have treated larvae as passive particles, with net downward transport resulting from gravitational sinking; others incorporate conditional downward swimming of larvae in response to light, gravity, or waterborne chemical cues (Butman, 1987; Butman *et al.*, 1988a; Eckman, 1990; Eckman *et al.*, 1994).

In this study, total swimming and sinking speeds were poor predictors of vertical movement. Competent larvae swam only 1.4 times faster than precompetent larvae but, due to behavioral differences, had rates of net vertical displacement that were 6 times higher. Despite swimming at similar speeds, precompetent larvae tended to meander throughout the experimental chambers, whereas competent
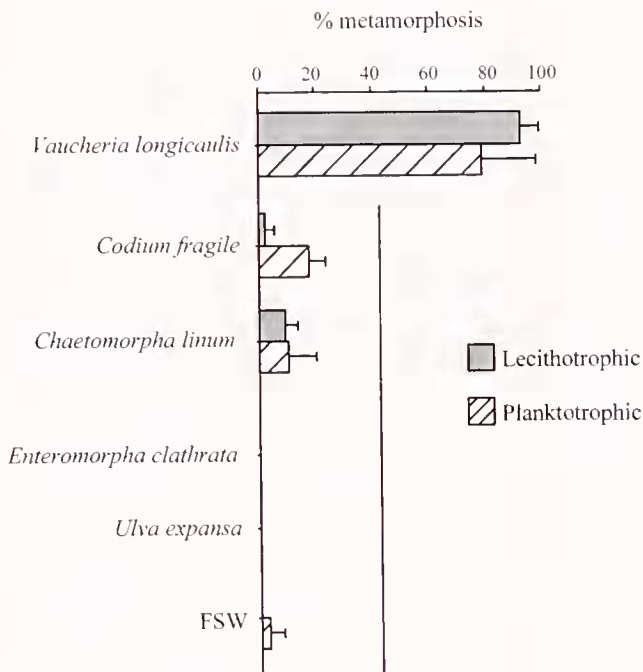
larvae had a strong directional bias resulting in rapid downward movement. By swimming towards the seabed, competent larvae can increase the probability of contacting an appropriate settlement site.

Although similar in size and passive sinking speeds, lecithotrophic and competent planktotrophic larvae of *Alderia modesta* exhibited subtle differences in path trajectories and vertical swimming speeds. Lecithotrophic larvae were more uniform in their behavior, and swam downward in faster, straighter paths that resulted in higher rates of vertical movement. In cultures, we observed these short-lived larvae making rapid excursions up into the water column and back down to the bottom, which may allow them to repeatedly sample the substratum during a brief dispersal period. Competent planktotrophic larvae were less consistent in their behavior, swimming with a significant downward bias but at a lower rate. This pattern may result from developmental variation during the month-long maturation period of planktotrophic larvae.

Surprisingly, few studies have documented vertical components of swimming behavior for taxa other than bivalves and crustaceans (Mileikovsky, 1973; Chia *et al.*, 1984). Bivalve larvae typically swim in vertically oriented helical spirals (Mann and Wolf, 1983; Mann *et al.*, 1991; Wang and Xu, 1997), and can lower their sinking rate, without altering swimming speed, by changing rotational velocity (Jonsson *et al.*, 1991). Downward swimming speeds were slower than rates of gravitational sinking in all bivalves examined, as in *A. modesta* and other taxa besides crustaceans (Chia *et al.*, 1984; Young, 1995). These data suggest that live larvae rarely move downward through passive sinking alone, but rather through a combination of gravity and behavior. Prior studies have not measured rates of net vertical displacement for populations of larvae, however. The present investigation demonstrates that larvae differing in ontogeny or life history can express behavioral differences that have potentially large consequences for stage-specific patterns of movement.

To place these data in an ecological context, we developed a numerical model based on sediment transport equations to examine the effects of sinking *versus* swimming on larval distributions (Fig. 4, and Komar, 1976; Gross *et al.*, 1992; Eckman *et al.*, 1994). To first order, the distribution of larvae above the bottom is governed by the same hydrodynamic principles (turbulent mixing and diffusion of momentum) that dictate vertical profiles of suspended sediment (Komar, 1976; Middleton and Southard, 1984). The magnitude of turbulent mixing relative to sinking or downward swimming determines the vertical position of larvae within a one-dimensional bottom boundary layer. We modeled the
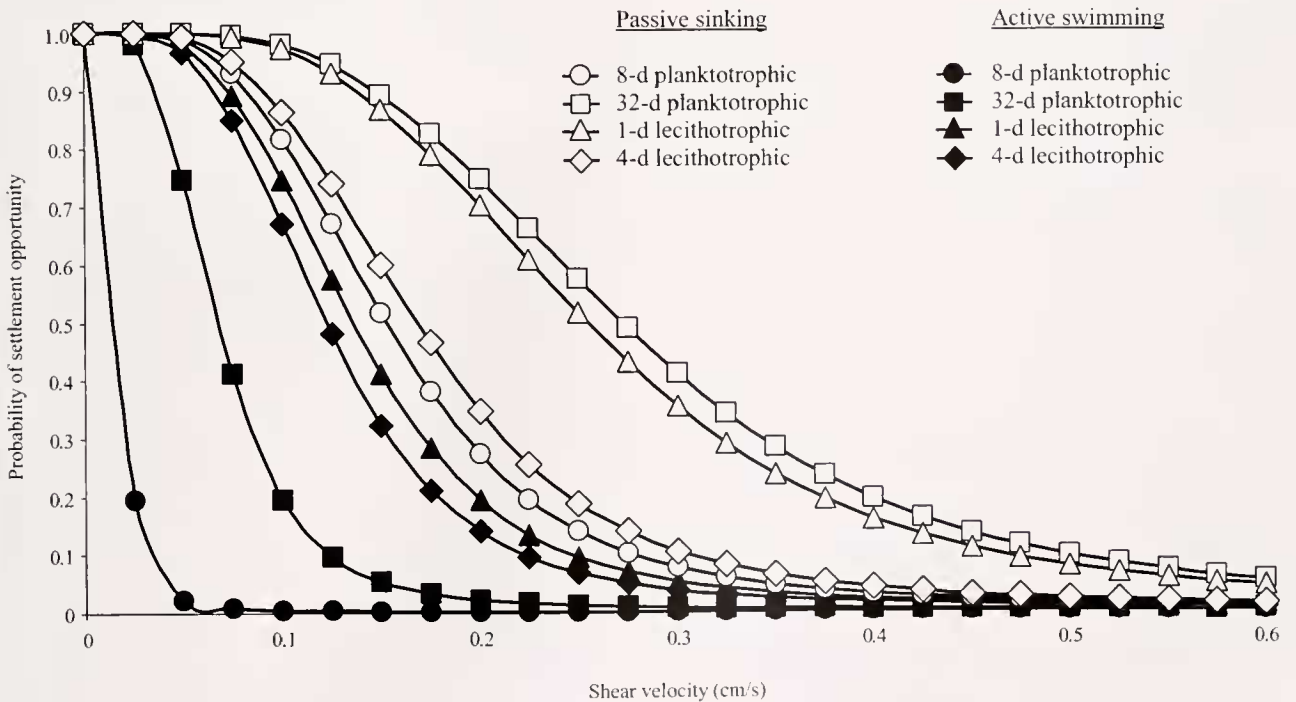

Figure 4. Numerical model of larval settlement opportunity, as a function of active swimming or passive sinking (see text for model description). Settlement opportunity is defined as the probability of a larva coming within one body length (200 μm) of the bottom, computed by vertically integrating larval distributions throughout the entire water column. Open symbols denote probabilities calculated using gravitational fall velocities of anesthetized larvae, and solid symbols represent probabilities calculated using rates of net vertical movement for actively swimming larvae.

equilibrium distribution of suspended larvae in the water column using the steady-state Rouse profile (equation 32, in Komar, 1976). The Rouse parameter indicates the strength of downward larval flux, due to passive sinking or active swimming, relative to the upward larval flux due to turbulent mixing (as characterized by the shear velocity). These profiles were then integrated over the entire water column (set at 1 m). Probability density functions were derived to describe the likelihood of an individual larva being suspended within one body length (200 μm) of the seabed for a given shear velocity. In the southern California estuaries inhabited by *A. modesta*, shear velocities typically range from 0.05 to 0.8 cm/s but are lower than 0.2 cm/s over most (70%) tidal cycles, and water depths at maximum flood tide are 1 m or less (Fingerut *et al.*, 2003). Net vertical displacement rates for live larvae (active) and sinking rates for anesthetized larvae (passive) were taken from Table 4.

Model outputs predicted substantially different results for actively swimming and passively sinking larvae. The concentration profiles generated for passively sinking lecithotrophic and competent planktotrophic larvae were essentially the same, because of comparable gravitational fall velocities. Larvae of both types were concentrated near the seabed at low intensities of turbulent mixing (Fig. 4). When rates of net vertical movement were used rather than sinking speeds, however, lecithotrophic larvae became more bottom-skewed in their distributions relative to competent planktotrophic larvae. A 2-fold difference in active, downward movement between the two types was magnified as a 5-fold difference in predicted concentrations along the bottom for shear velocities commonly found in the field.

The consequences of active swimming *versus* passive sinking were even greater for precompetent larvae (Fig. 4). Anesthetized, 8-d-old larvae sank at −0.9 mm/s, comparable to the downward movement of swimming lecithotrophic veligers. When the passive fall velocity of 8-d-old larvae was used to establish their distribution, the model predicted that most precompetent larvae would sink to the bottom at shear velocities less than 0.2 cm/s. However, when their rate of net vertical displacement (−0.10 mm/s) was used instead, 8-d-old larvae were predicted to mix throughout the water column at most shear velocities. The life-history strategy of planktotrophy requires precompetent larvae to remain suspended for feeding. Although passive sinking would carry newly hatched larvae to the bottom, active swimming will keep such larvae distributed throughout the water column, where they function as dispersing propagules. The behavior of free-swimming larvae must therefore be taken into account when modeling transport and settlement, as swimming speeds and sinking rates do not accurately represent patterns of vertical movement for different developmental stages. Although based on still-water analyses, our data suggest patterns of larval movement to be expected in turbulent water; future studies in sheared flows

are needed to test these predictions of behavior and transport for *A. modesta* larvae (Grunbaum and Strathmann, 2003).

It remains controversial at what scale and for which processes larvae can be effectively modeled as passive particles. At least in slower flow regimes, taxonomically diverse larvae and meiofaunal organisms can distribute themselves selectively in the water column and settle in or on preferred substrates along the bed (Butman *et al.*, 1988b; Pawlik and Butman, 1993; Fingerut *et al.*, 2003; Ullberg and Olafsson, 2003). Moreover, experimental studies on larvae of two unrelated molluscs, the Eastern oyster *Crassostrea virginica* and the opisthobranch *Alderia modesta*, reported a remarkably similar suite of behavioral responses to dissolved cues. Larvae of both species increased turning rates, decreased swimming speeds, and swam primarily downward upon stimulation with habitat cues in the water column (Tamburri *et al.*, 1992, 1996; Krug and Zimmer, 2000). These findings are consistent with the present results for competent larvae—those with a biological imperative to stay near the bottom and locate a settlement site. Although passive sinking would seem more effective at bringing larvae into contact with the seabed, live larvae opt to swim rather than sink. This behavior may allow larvae to change their distribution rapidly in response to physical and chemical cues, providing a distinct advantage during habitat selection over random, passive encounters with the bottom (Browne and Zimmer, 2001).

Consequences of developmental dimorphism for dispersal potential and habitat colonization

Developmental dimorphisms are maintained in populations by trade-offs between the advantages of dispersal and costs to the migratory morph (Roff, 1986, 1996; Langellotto *et al.*, 2000). Winged insect morphs can disperse through the air, locating high-quality resources and colonizing habitats after disturbances; however, due to costs of constructing and fueling large flight muscles, winged females have lower fecundities and winged males produce fewer mating calls than wingless conspecifics (Denno *et al.*, 1980, Roff and Fairbairn, 1991; Mole and Zera, 1993; Tanaka 1993; Crnokrak and Roff, 1995; Langellotto and Denno, 2001). Plants that colonize unpredictable environments often produce two types of seeds, one dropping near the parent and the other expressing a structure that can increase drag on a falling seed to aid dispersal by wind (Morse and Schmitt, 1985; Venable, 1985; Venable and Levin, 1985; Telenius and Torstensson, 1989; Imbert, 1999). Some coastal plants have dimorphic fruit segments, parts of which have a buoyant coat that increases dispersal in water (Payne and Maun, 1981). Dispersing seeds may have a reduced capacity for dormancy and phenotypic plasticity as adult plants, how-

ever (Venable and Levin, 1985, Telenius and Torstensson, 1989; Zhang, 1995).

In contrast to terrestrial examples cited above, in marine organisms dispersal dimorphisms involve altered time to competence or settlement preference among larvae, rather than changes in gross morphology (Chia *et al.*, 1996). Larval dispersal by ocean currents is an unavoidable consequence of development occurring in the water column and requires only minor adaptations for long-distance travel (Pechenik *et al.*, 1984; Strathmann, 1985). Physical differences between water and air contribute to the different dispersal strategies of marine and terrestrial organisms. Seawater is 850 times denser than air, providing a buoyant force for suspended organisms, and its 60-fold higher dynamic viscosity results in lower sinking rates for planktonic *versus* airborne particles (Power, 1989; Strathmann, 1990). Due to their physical environment, eggs and larvae of marine organisms can increase flotation by altering ionic or lipid composition, or counteract sinking by increasing drag through simple modifications of ciliated bands or velar lobes (Lambert and Lambert, 1978; Emlet, 1983; Chia *et al.*, 1984; Kelman and Emlet, 1999). Dimorphisms can therefore alter the dispersal potential of marine larvae by changing time to attainment of competence, without major alterations in bodily form or function.

One goal of this study was to compare traits relevant to dispersal and habitat colonization for long-lived, feeding larvae and short-lived, nonfeeding larvae of the same marine animal. Lecithotrophic larvae of *Alderia modesta* metamorphose within 2 d of hatching when *Vaucheria longicaulis* is present, but most die after a week if the alga is not encountered, thus limiting their dispersal potential (Krug, 2001). Extending the larval period by even a few days can result in high mortality and post-metamorphic costs for nonfeeding larvae, which may thus be under selective pressure to locate a high-quality settlement site quickly (Pechenik, 1999). Strong downward swimming should concentrate lecithotrophic larvae of *A. modesta* near the bed, increasing the likelihood of contact with *V. longicaulis* while minimizing the risks of transport from the natal habitat.

In contrast, planktotrophic larvae must survive a 4-week dispersal period before locating and settling in an appropriate environment. Based on drogue studies, Levin (1983) concluded that larvae with a planktonic phase longer than 3 weeks could exit Mission Bay (San Diego, CA) and be transported by along-shore currents. Populations of *A. modesta* are genetically homogenous from San Diego to Tomales Bay, California, indicating that exchange of larvae occurs between estuaries (Ellingson and Krug, unpubl. data). Adult *A. modesta* produce 10-fold more planktotrophic than lecithotrophic larvae (~300 *vs.* 30 larvae per clutch; Krug, 1998), but planktotrophic larvae face a high mortality rate. Only a small percentage of planktotrophic larvae are likely

to reach competence, but the survivors have the potential to disperse and colonize distant patches.

In terms of overall size and swimming ability, mature planktotrophic and newly hatched lecithotrophic larvae of *A. modesta* were remarkably similar. Strikingly, competent larvae of both modes exhibited the same shadow response, which was absent in precompetent larvae. Such responses are known from a range of invertebrate taxa (Forward, 1984; Young and Chia, 1985; Buskey *et al.*, 1986), but their ecological significance remains unclear. This behavior is yet another response to an environmental cue that is shared by both types of competent larvae. In a prior study, both types of larvae exhibited qualitatively similar changes in behavior when stimulated with waterborne settlement cues from the host alga (Krug and Zimmer, 2000). Thus, both planktotrophic and lecithotrophic development converge on a phenotypically similar state of competence in this species.

Habitat selection occurs when competent larvae settle to the bottom and then initiate metamorphosis. No differences were observed between the two types of larvae of *A. modesta* in their degree of settlement specificity: competent larvae metamorphosed on the host alga *V. longicaulis*, and not on other macroalgae. Lecithotrophic larvae were previously shown to exhibit a high degree of specificity for the host-associated cue, metamorphosing in response to *V. longicaulis* but not to 17 alternative macroalgae (Krug, 2001). Limited availability of competent planktotrophic larvae precluded testing as many algal species, but long-lived larvae appear similarly able to differentiate among potential habitat cues. The one notable difference was that planktotrophic larvae rarely underwent spontaneous metamorphosis upon reaching competence, as larvae from some lecithotrophic clutches do in the first day after hatching (Krug, 2001). This trait is likely an adaptive response to the different dispersal strategies of the two development modes. Lecithotrophic larvae emerge in a suitable habitat, so combining spontaneous and *Vaucheria*-dependent metamorphosis is a viable bet-hedging dispersal strategy. In contrast, planktotrophic larvae may end up far from a good habitat after their month-long development, and consequently must delay metamorphosis until encountering the *Vaucheria*-associated cue.

In summary, competent planktotrophic and lecithotrophic larvae of *Alderia modesta* are qualitatively similar in swimming behavior and patterns of vertical movement, in their responses to light and waterborne chemical settlement cues, and in their metamorphic requirements. Selection for host-specific colonization has evidently preserved a common suite of traits in alternative developmental pathways, despite the radically different dispersal potentials of the two types. Nevertheless, small differences between the two types of larvae (in rates of net vertical displacement or spontaneous metamorphosis) may represent fine-tuning of

traits important in habitat selection, within the constraints imposed by their respective dispersal strategies.

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